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Food-Web Dynamics in Three Seagrass Systems in Caramoan Peninsula, Philippines

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Abstract Ecopath with Ecosim (EWE) modeling software was used in constructing steady-state trophic models of three diverse seagrass ecosystems to analyze the impact of biomass changes in each component of the ecosystems. The food web models were utilized to make predictions and management options regarding the impacts of biomass alterations in three varied actual scenarios: (1) pristine, isolated, and sheltered seascape; (2) increased connectivity with mangroves; and (3) increased connectivity with corals. The Mixed Trophic Impact (MTI) analysis was utilized to identify consumer compartments' cumulative effects on the producer compartment (i.e., seagrass). The stability and resilience of the seagrass systems were inferred from the network flow indices as the biomass functions. Then, the models were subjected to multiple dynamic simulations. The hypothesis is that the three different scenario simulations resulted in varied biomasses and trophic interactions that revealed insights towards possible management options of the seagrass systems in Caramoan Peninsula, Philippines. Results revealed that although all the seagrass systems are immature, the pristine, isolated, and sheltered seascape (Site A, Lipata Bay) should be given more management owing to its vulnerability that the presence or connectivity cannot afford with other ecosystems (e.g., coral reefs and mangroves). The seagrass meadow nearest to the mangrove forest (Site B, Manlawi Bay) needs unique management to maximize its potential as a refuge for crustaceans and other economically important invertebrates. The seagrass meadow closest to the coral reefs (Site C, Hurandayan Bay) can also be considered conservation sentinels since it is less susceptible to stress-induced changes and can recover from unexpected perturbations than the other seagrass meadows.

Keywords Caramoan Peninsula, Dynamic Models, Philippines Seagrass, Trophic Models

1. Introduction

Seagrass meadows are valuable ecosystems because of the benefits of the services they provide. The diversity and productivity of coastal ecosystems are attributed to the presence of these marine angiosperms [1]. They are habitats and food for many organisms in littoral zones of tropical and temperate regions [2]. Larger animals consume the invertebrate assemblages that graze and feed in seagrass beds. It illustrates the complex links of the food web between seagrass, fishes, and other marine animals as higher trophic-level organisms. However, there remain knowledge gaps on the interactions between seagrass and their consumers [3]. The biology of seagrasses in the Philippines was studied extensively focusing on distribution, phenology, sexual reproduction, and sediment effects [4]. However, there is a scarcity of trophic modeling on seagrass systems, hence, seagrass production transmission to higher-order consumers in near-shore food webs remains unresolved. This knowledge void is more prominent when we consider the influence of the presence or absence of other marine ecosystems like corals and mangroves on a nearby seagrass system.

Trophic cascades based on changes in biomass are difficult to demonstrate in seagrass ecosystems. Very few studies have quantified energy transfer from the seagrass

into marine food webs, although much of the primary production in marine ecosystems is generated by seagrasses along with the production of phytoplankton, algae, and mangroves. This trophic modeling study on the seagrass meadows of Caramoan Peninsula in various scenarios using is one of the few endeavors that aimed to provide clues to the gaps in knowledge on the influence of the other ecosystems on the seagrass food webs.

Theoretically, there are two major food chains within an ecosystem: the grazing and the detrital food chains, which differ in terms of their energy source for the initial consumers. In a grazing ecosystem, the primary source of energy for the initial consumer is the autotrophs or living plant tissues, while in the detrital food chain, the energy source for the initial consumers (bacteria and fungi) is the dead organic matter or detritus. The flow is directional in the grazing food chain, with net primary production providing carnivores' energy. The flow is not unidirectional in the decomposer food chain; the waste materials and detritus in each consumer trophic level are recycled, returning as an input to the detritus at the food base chain. The two major food chains: grazing and detrital food chains, can be combined to produce a generalized trophic structure and energy flow through an ecosystem [5].

Quantifying energy flux through the ecosystem requires evaluating the consumption, ingestion, assimilation, respiration, and production at each trophic level. Within the seagrass system's food webs, the trophic level represents seagrasses and their consumers' position. Seagrass biomass enters the second trophic level by either secondary production through grazing, recycling of biomass by the detrital loops, or feeding on phytoplankton by certain species as early-stage larvae. Outputs of biomass happen at all trophic levels from predation and mortalities [6].

In the seagrass system, the waste products from the grazing food chain provide an initial energy source for the decomposer food chain. The two food chains are also linked via the process of predation. Aside from the breaking down of dead organic matter, decomposer organisms are also food for numerous other animals [7].

The present study aims to construct three trophic models using the Ecopath with Ecosim (EwE) software in three ecologically varied seagrass systems in Caramoan Peninsula, Philippines. The ecological differences of seagrass systems were based on three actual scenarios: (1) pristine, isolated, and sheltered seascape (Site A, Lipata Bay); (2) increased connectivity with mangroves (Site B, Manlawi Bay); and (3) increased connectivity with corals (Site C, Hurandayan Bay). The systems' trophic interactions were simulated by varying biomasses of the functional groups within the systems.

Caramoan Peninsula is one of the Philippines' under-researched areas. The pristine seagrass ecosystems in this part of the country are ideal sites for trophic analysis by characterizing the ecosystem components and links, especially between the primary producers and the consumers in seagrass systems [8].

This study builds on Lindeman's tropho-dynamics concept [8] by examining how energy flows from the seagrasses to their consumers. “Trophodynamics, by regulating the cycling of mass, energy, and nutrients, determines how marine ecosystems function and respond to both internal and external pressures, as food web pathways adapt to facilitate ecosystem resilience and persistence” [9]. By using models as tools to depict trophic flows among the functional groups in the system, this study derived insights the into seagrass structure's energy dynamics. Thus, in simulating the constructed models, the current study could determine the patterns of magnitude and variability of detrital and herbivory pathways in the seagrass systems whose isolation or proximity with other ecosystems (corals and mangroves) enhance or limit their role as a refuge and food source on seagrass production.

Studies that have quantified the energy flows from seagrasses to coastal food webs [10] highlighted the crucial link between the primary production of seagrasses and the other major plant groups [11]. With the scarcity of studies on trophic modeling in seagrass systems, the present study's findings may provide the information needed to understand how living aquatic resources' sustainability depends on the ecosystem structure and function in general, and the trophic structure and biomass flows through species interaction [12].

2. Materials and Methods

2.1. Study Site

Biomass sampling of the seagrass ecosystem components was conducted from October 2021 to October 2022. Three locations were pre-selected: (1) pristine, isolated, and sheltered seascape (Site A, Lipata Bay); (2) increased connectivity with mangroves (Site B, Manlawi Bay); and (3) increased connectivity with corals (Site C, Hurandayan Bay) (Figure 1) Site A (Lipata Bay) has an estimated overall seagrass cover of 85 to 95% (composed of *Syringodium isoetifolium, Halodule uninervis Cymodocea serrulata, Cymodocea rotundata,* and *Enhalus acoroides*), a muddy sand substrate type, and a very low degree of disturbance from gleaners (Figure 2a). Site B (Manlawi Bay) has an estimated overall seagrass cover of 50% (composed of *C. serrulata* and *E. acoroides*), a dominantly muddy substrate type, and with a low to moderate degree of disturbance from gleaners (Figure 2b). Site C (Hurandayan Bay) has an estimated overall seagrass cover of 75% (composed of *Thalassia hemprichii, S. isoetifolium, C. serrulata, rotundata,* and *E. acoroides*), a combination of sandy and rubble death substrate type, and a very low degree of disturbance from gleaners (Figure 2C).

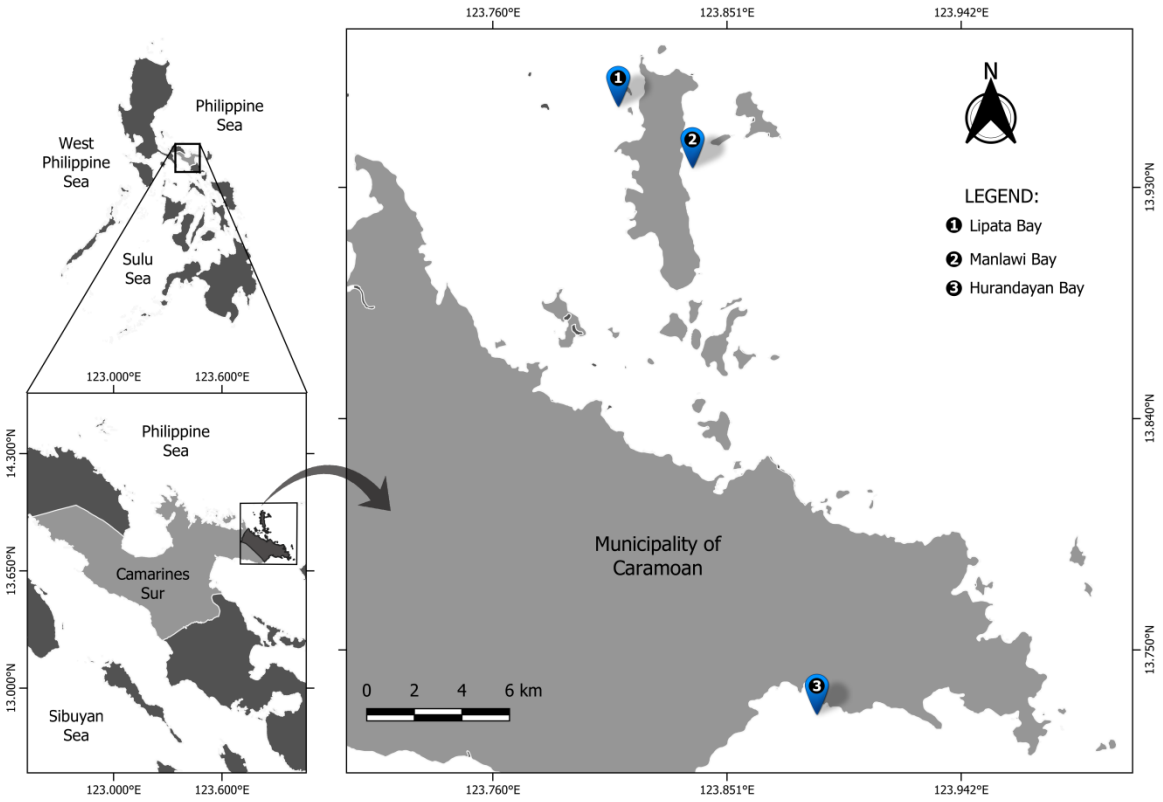


Figure 1. Location of study sites

2.2. Sampling and Sample Analysis

At each site, transect field sampling was done in the mixed seagrass. For each site, three sampling stations were established that represent the bay area. In each station, three transects were laid, thus a total of 9 transects in each site. A 20-cm corer was used to obtain seagrass samples. To estimate the biomass of seagrasses and fauna was estimated using a 20-cm corer and a trawl method. At least 10 to 20 core samples were collected every 10 meters along each transect. Therefore, during each sampling time, total grab samples were taken over a point-to-point distance of ~10 m in the form of 100-m and 200-m transects perpendicular to the shoreline.

The collection was done during the lowest tidal level from the seagrass bed's boundary starting from at least 10-15 m landwards limit to avoid edge effects. A 500 mm mesh was used to sieve core samples. Samples were identified up to the lowest taxon or functional groups. Epiphytes in the seagrass samples were scraped before weighing to determine their wet weights (g ww m^2). A sturdy sampler beam trawl was also used to collect other epifauna [13].

Figure 2a. Study A, Lipata Bay

Figure 2b. Study B, Manlawi Bay

Figure 2c. Study C, Hurandayan Bay

Sampling was done during the day and night-time during wet (June to November) and dry (December to May) seasons. First, each sample biomass (g ww m^2) was determined to estimate the total annual biomass (t km^{-2} y^{-2}). To determine the diet matrix structure for the groups required for ecological modeling using Ecopath with Ecosim and Ecospace (EwE) [14], dietary analysis composition was obtained from the literature.

2.3. Modeling and Analysis Approach

The seagrass systems' models were constructed in Ecopath with Ecosim (EwE) EwE 6.6.3 [12]. The EwE software has essential routines for the study of aquatic ecosystems: the Ecopath [12, 14-15], Ecoranger and sensitivity analysis [16]; Ecospace and Ecosim [17]; keystone species [18], among others.

The diet items of functional groups were based on the literature [19], and other available literature. The diet compositions were estimated based on each prey item's relative abundance in the sites. The production/biomass ratio for a functional group (P/B) and the ratio of the consumption to biomass for predators (Q/B) of the functional groups were based on the values reported in the literature, and by using the approach suggested by Christensen and Walters [16].

Input for EwE includes biomass (B) per compartment, ratios of Productivity: Biomass (P B^{-1}) and Consumption: Biomass (Q B^{-1}), and a proportion of unassimilated food, and/or some combined variable (e.g., Gross food conversion Efficiency (GE as PB/QB)). The biomass values given as (t km^{-2} y^{-2}) derived from field data were used, while other parameter values were based on the literature.

To avoid bias in estimating parameter values, the initial inputs are introduced into the Ecoranger routine of EwE. Monte Carlo simulations were used to generate a theoretical frequency distribution. The models which have parameters close to the overall mean were selected after the 10,000 model runs and 200 fitting models for various scenarios were done.

Models were balanced by adjusting the inputs until Ecotrophic Efficiency (EE) does not exceed 1. EE values that are less than 1 mean biomass excess that accumulates in the system or is exported out or diminished by other forms of mortality. Biomass, P/B, Q/B ratios, and diet matrix were entered as inputs. Imbalanced models were initially constructed as indicated by EEs with a value which is more than 1 and interpreted that these groups have a high demand to be sustainable [17]. Important outputs are the trophic levels of the functional groups. Diet compositions were adjusted if the outputs deviated from the expected results [16].

To assess the structure, stability, maturity, and networks of the ecosystems, the Ecosystem Network Analysis was used. This approach is based on the Ecopath outputs of effective trophic level [20], the Mixed Trophic Impact (MTI) matrix [21], and Omnivory Index [22].

Ecosim modeling was done by simulating a series of forcing scenarios to explore changes in the functional groups' biomass as a response to pre-determined conditions: (1) pristine, isolated, and sheltered seascape; (2) decreased connectivity with corals and mangroves; and (3) increased connectivity with corals and mangroves. In the simulations, vulnerability parameter (v) [16] was manipulated to evaluate how density-dependent controls and predation affect the standing stocks of functional groups that exist in each of the three conditions.

Thus, the initially constructed Ecopath models were used to build Ecosim models that focus on three simulations routines: (1) Applying forcing function (primary producer), (2) Applying forcing function (consumer), and (3) Predicting consumption, were done in three specific simulation scenarios:

Scenario 1 – Effects of simulated bottom-up control mechanisms

Scenario 2 – Effects of simulated top-down control mechanisms.

Scenario 3 – Effects of simulated mixed-flow control mechanisms

In all three scenarios, the Group Information includes Seagrasses Maximum Relative P/B = 2.0; Grazers Maximum Relative Feeding Time=2.0; Grazers Feeding Time Adjustment Rate=0.5; Predator Effect on Feeding Time = 0.0, and Duration of simulation: 10 years. But for Scenario 1, the Vulnerability (ν) setting was changed: (Scenario 1: ν=1.0; Scenario 2: ν=6.0 and Scenario 3: ν=2.0). The three scenarios were designed to test how possible changes to one of the levels in the trophic structure or food web or chain can result in changes in other levels (i.e., trophic cascade). Trophic cascades typically impact trophic levels below an altered level or levels above the altered level. The directional cascades are categorized as either top-down or bottom-up control to mean that an alteration to a certain food chain occurred at either the top trophic level or the bottom trophic level and eventually impacted the other levels up or down the food chain.

3. Results

3.1. Trophic Structure

In Tables 1a, 1b, and 1c, the maximum TL in the system is that of *Protoreoaster nodosus* (TL = 3. 92) in Site A (Lipata Bay), and crustaceans in Sites B (Manlawi Bay) (TL = 2.76) and Site C (Hurandayan Bay) (TL =3.0), which both are the top predators in the three seagrass meadows. Overall, the seagrass systems have a low mean trophic level of 1.728 (Site A), 1.63 (Site B), and 1.86 (Site C) indicating short food chain and lack of top predators in the system. Tables 2a, 2b, and 2c present the diet matrices that were entered as inputs

It is expected that primary producers will have relatively higher EE values than top predators. However, for the seagrass systems in Caramoan Peninsula, the EE values are high for most of the consumers (Table 1a), indicating that these groups have a crucial role in the food web and maybe challenged by high predation risk.

The relatively low EE values for the detritus group (0.02 for Site A, 0.13 for Site B, and 0.09 for Site C) indicate that the consumption is exceeded by biomass accumulation. Based on the values, more accumulation was observed in Site B (Manlawi Bay) which is the site nearest to the mangroves. The lower EE values for seagrasses suggest that there are few grazers in the ecosystems. Low EE value for the other invertebrate benthic groups in the three meadows indicates the groups were not fully consumed. Thus, the three seagrass systems have ecological efficiency [22], indicating a significant amount of energy available for transfer in the food chain.

Comparison of the three sites: (1) pristine, isolated, and sheltered seascape (Site A, Lipata Bay); (2) increased connectivity with mangroves (Site B); and (3) increased connectivity with corals (Site C), showed that Site A and C has 15 to 16 functional groups compared with Site B with only 8 functional groups. Biomass of seagrasses was highest in Site B, the meadow nearest to the mangroves, although only two seagrass species are present, while both Sites A (the pristine, isolated meadow) and Site C (near the coral reefs) have both five species present. Site C has the highest total biomass (excluding detritus) of 417 t km^2, while Site A has the least total biomass of 347 t km^2.

Table 1a. Basic inputs and estimated outputs (bold) of Site A (Lipata Bay, Lahuy Is., Caramoan Peninsula) seagrass system model

	Group name	TL	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	Predat Mort	Other mort	Flow to detritus
1	*Proteroaster nodosus*	2.92	2.700	0.52	2.60	0.95	0.20	---	0.03	1.47
2	*Synapta maculata*	2.78	0.610	2.80	5.60	0.95	0.50	8.31	0.14	0.77
3	Nematodes	2.56	1.600	3.80	12.50	0.28	0.30	1.07	2.73	8.37
4	*Linckia spp*	2.38	0.082	0.52	2.60	0.95	0.20	32.56	0.03	0.04
5	*Diadema* spp.	2.28	0.360	4.45	22.25	0.66	0.20	2.93	1.53	2.15
6	Polychaetes	2.00	4.200	1.63	12.46	0.01	0.13	0.01	1.62	17.28
7	*Tripneustes gratilla*	2.00	0.290	4.47	25.00	0.95	0.18	6.52	0.22	1.52
8	Zooplankton	2.00	2.870	67.00	192.00	0.95	0.35	1.39	3.35	119.8
9	*Syringodium isoetifolium*	1.00	22.92	8.43	---	0.06	---	0.49	7.94	182.0
10	*Halodule uninvervis*	1.00	20.17	8.43	---	0.01	---	0.06	8.38	168.9
11	*Cymodocea serrulata*	1.00	35.00	8.43	---	0.05	---	0.45	7.98	279.3
12	*Cymodocea rotundata*	1.00	35.00	8.43	---	0.05	---	0.45	7.98	279.3
13	*Enhalus acoroides*	1.00	37.70	8.43	---	0.05	---	0.41	9.03	302.6
14	Phytoplankton	1.00	30.42	67.00	---	0.08	---	2.42	28.00	5152
15	Detritus	1.00	19.80	---	---	0.02	---	---	---	---

TL, trophic level; B, biomass (t wet weight (WW) km^{-2}); P/B, production/biomass ratio or the instantaneous rate of total mortality (Z) (yr^{-1}); Q/B, consumption/biomass ratio or consumption rate (yr^{-1}); EE, ecotrophic efficiency, P/Q, production/consumption ratio or gross efficiency; Predat, predator; mort, mortality; Flow to detritusis in t WW km^{-2} yr^{-1}.

Table 1b. Basic inputs and estimated outputs (bold) of Site B (Manlawi Bay, Lahuy Island, Caramoan Peninsula) seagrass system model

	Group name	TL	B ($t\ km^{-2}$)	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	Predat Mort	Other mort	Flow to detritus
1	Crustaceans	2.76	0.180	4.93	14.50	0.95	0.34	---	0.25	0.57
2	Nematodes	2.30	1.600	3.80	12.50	0.09	0.30	0.326	3.47	9.56
3	*Tripneustes gratilla*	2.00	1.840	4.47	25.00	0.06	0.18	0.284	4.19	16.90
4	Zooplankton	2.00	15.17	67.00	192.00	0.01	0.35	0.447	66.55	1592
5	*Cymodocea serrulata*	1.00	50.00	8.43	---	0.05	---	0.396	8.034	401.7
6	*Enhalus acoroides*	1.00	150.0	8.43	---	0.01	---	0.119	8.311	1247
7	Phytoplankton	1.00	30.42	67.00	---	0.37	---	11.14	19.28	3547
8	Detritus	1.00	19.80	---	---	0.13	---	---	---	---

TL, trophic level; B, biomass (t wet weight (WW) km^{-2}); P/B, production/biomass ratio or the instantaneous rate of total mortality (Z) (yr^{-1}); Q/B, consumption/biomass ratio or consumption rate (yr^{-1}); EE, ecotrophic efficiency, P/Q, production/consumption ratio or gross efficiency; Predat, predator; mort, mortality; Flow to detritusis in t WW km^{-2} yr^{-1}.

Table 1c. Basic inputs and estimated outputs (bold) of Site C (Hurandayan Bay, Guijalo, Caramoan Peninsula) seagrass system model

	Group name	TL	B ($t\ km^{-2}$)	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	Predat Mort	Other mort	Flow to detritus
1	Crustaceans	3.00	0.18	4.93	14.50	0.95	0.34	---	0.25	0.57
2	*Proteroaster nodosus*	2.92	0.24	0.52	2.60	0.00	0.20	---	0.52	0.25
3	*Synapta maculata*	2.78	0.06	2.80	5.60	0.95	0.50	72.93	0.14	0.08
4	Nematodes	2.56	1.60	3.80	12.50	0.71	0.30	0.27	3.53	9.65
5	*Linckia spp*	2.42	0.08	0.52	2.60	0.95	0.20	24.12	0.03	0.05
6	*Diadema* spp.	2.28	0.36	4.45	22.25	0.22	0.20	0.99	3.47	2.85
7	Polychaetes	2.00	1.50	1.63	12.46	0.12	0.13	0.19	1.44	5.90
8	*Tripneustes gratilla*	2.00	1.84	4.47	25.00	0.05	0.18	0.23	4.24	17.01
9	Zooplankton	2.00	15.1	67.00	192.00	0.00	0.35	0.30	66.70	1594
10	*Thalassia hemprichii*	1.00	37.06	8.43	---	0.03	---	0.23	8.21	304.1
11	*Syringodium isoetifolium*	1.00	22.92	8.43	---	0.04	---	0.37	8.07	184.9
12	*Cymodocea serrulata*	1.00	50.00	8.43	---	0.03	---	0.28	8.15	407.3
13	*Cymodocea rotundata*	1.00	52.20	8.43	---	0.03	---	0.27	8.16	425.8
14	*Enhalus acoroides*	1.00	50.00	8.43	---	0.03	---	0.28	8.15	407.3
15	Phytoplankton	1.00	30.42	67.00	---	0.42	---	12.71	17.71	3258
16	Detritus	1.00	19.80	---	---	0.09	---	---	---	---

TL, trophic level; B, biomass (t wet weight (WW) km^{-2}); P/B, production/biomass ratio or the instantaneous rate of total mortality (Z) (yr^{-1}); Q/B, consumption/biomass ratio or consumption rate (yr^{-1}); EE, ecotrophic efficiency, P/Q, productio /consumption ratio or gross efficiency; Predat, predator; mort, mortality; Flow to detritusis in t WW km^{-2} yr^{-1}.

Table 2a. Diet composition matrix for all function groups of Site A (Lipata Bay, Lahuy Island, Caramoan Peninsula) seagrass system model

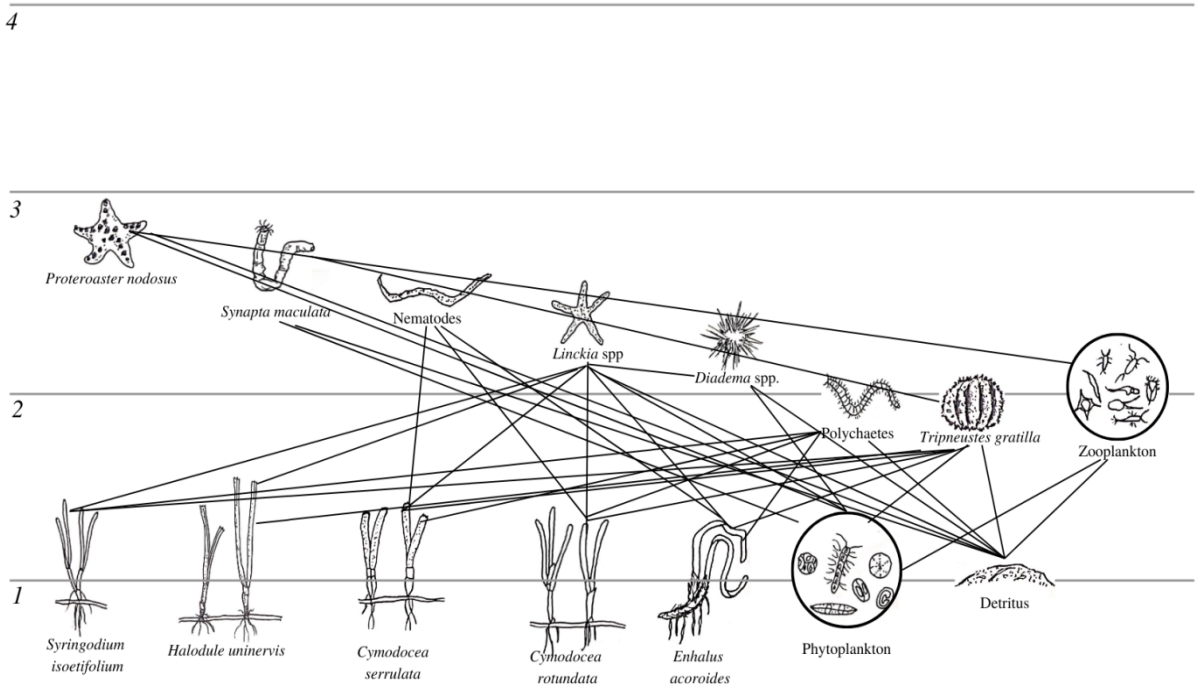
		Predator							
	Prey	1	2	3	4	5	6	7	8
1	*Proteroaster nodosus*	0.15							
2	*Synapta maculata*		0.50	0.20	0.07				
3	Nematodes	0.15							
4	*Linckia spp*	0.15			0.07	0.20			
5	*Diadema* spp.								
6	Polychaetes	0.25			0.16				
7	*Tripneustes gratilla*								
8	Zooplankton			0.20	0.10				
9	*Syringodium isoetifolium*				0.10		0.20	0.10	
10	*Halodule uninervis*				0.10			0.15	
11	*Cymodocea serrulata*			0.20	0.10		0.20	0.18	
12	*Cymodocea rotundata*			0.20	0.10		0.20	0.17	
13	*Enhalus acoroides*			0.20	0.10		0.20	0.10	
14	Phytoplankton	0.15	0.25		0.10	0.20		0.15	0.80
15	Detritus	0.15	0.25		0.10	0.60	0.20	0.15	0.20

Table 2b. Diet composition matrix for all function groups of Site B (Manlawi Bay, Lahuy Island, Caramoan Peninsula) seagrass system model

		Predator			
	Prey	1	2	3	4
1	Crustaceans				
2	Nematodes	0.20			
3	*Tripneustes gratilla*	0.20			
4	Zooplankton	0.30	0.30		
5	*Cymodocea serrulata*		0.30	0.30	
6	*Enhalus acoroides*		0.20	0.30	
7	Phytoplankton	0.15	0.10	0.20	0.70
8	Detritus	0.15	0.10	0.20	0.30

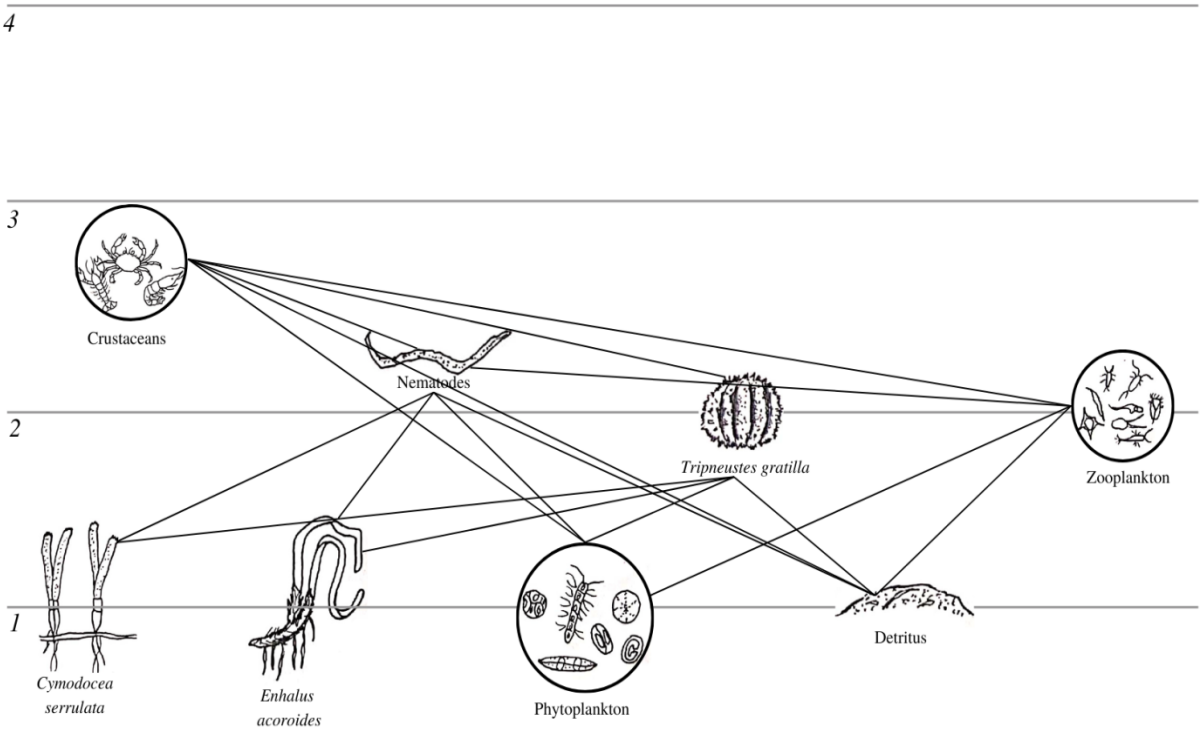
Table 2c. Diet composition matrix for all function groups of Site C (Hurandayan Bay, Guijalo, Caramoan Peninsula) seagrass system model

		Predator								
	Prey	1	2	3	4	5	6	7	8	9
1	Crustaceans									
1	*Proteroaster nodosus*									
2	*Synapta maculata*	0.10	0.15		0.20	0.10				
3	Nematodes	0.10		0.50						
4	*Linckia spp*	0.10	0.15			0.10	0.20			
5	*Diadema* spp.	0.10	0.15							
6	Polychaetes	0.10				0.10				
7	*Tripneustes gratilla*	0.10	0.25							
8	Zooplankton	0.20			0.20					
9	*Thalassia hemprichii*					0.10		0.10	0.14	
10	*Syringodium isoetifolium*					0.10		0.10	0.14	
11	*Cymodocea serrulata*				0.20	0.10		0.20	0.14	
12	*Cymodocea rotundata*				0.20	0.10		0.20	0.14	
13	*Enhalus acoroides*				0.20	0.10		0.20	0.14	
14	Phytoplankton	0.10	0.15	0.25		0.10	0.20		0.15	0.80
15	Detritus	0.10	0.15	0.25		0.10	0.60	0.20	0.15	0.20



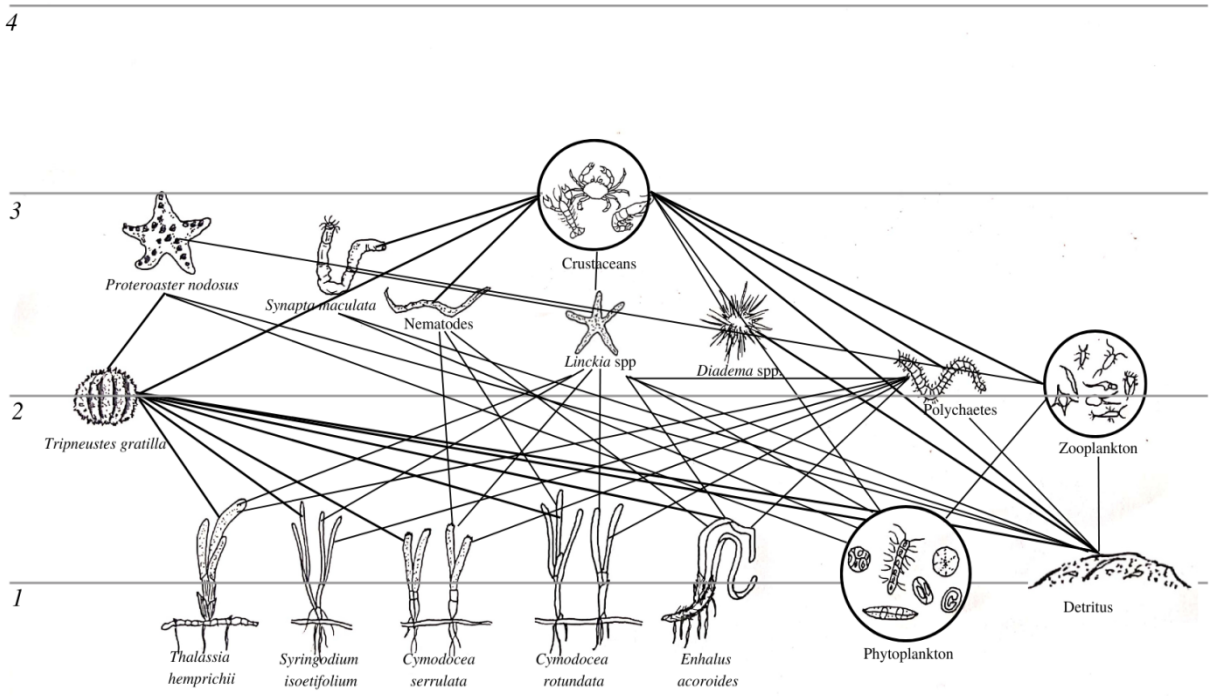
The lines show food connectivity. All flows are expressed in t km^{-2} $year^{-1}$.

Figure 3a. Trophic interaction in Site A (Lipata Bay, Lahuy Island, Caramoan Peninsula) seagrass system model



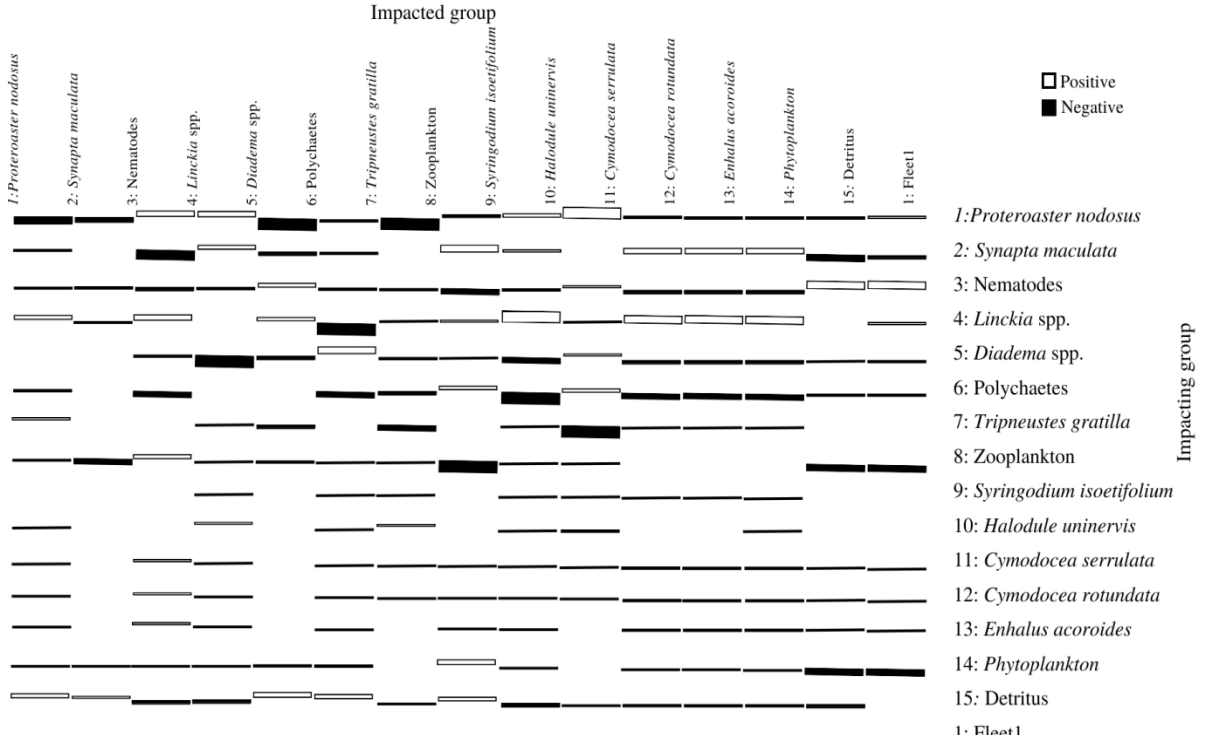
The lines show food connectivity. All flows are expressed in t km^{-2} $year^{-1}$.

Figure 3b. Trophic interaction in Site B (Manlawi Bay, Lahuy Island, Caramoan Peninsula) seagrass system model



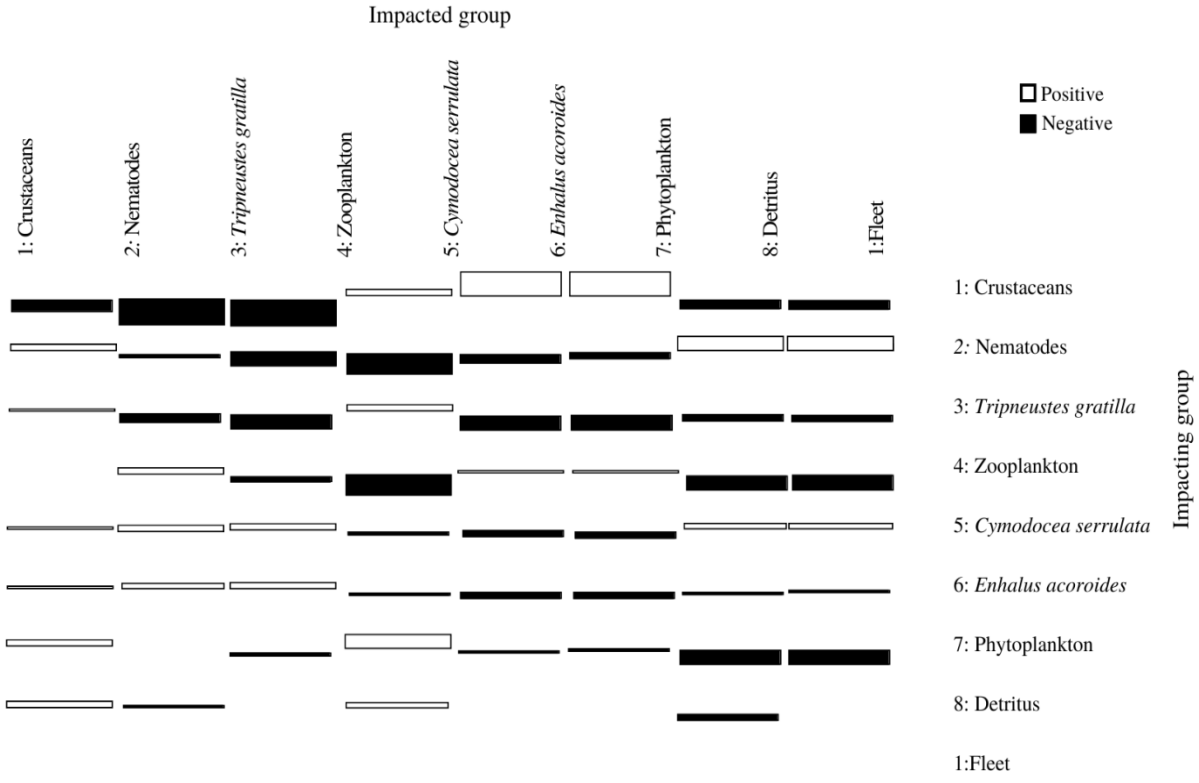
The lines show food connectivity. All flows are expressed in t km^{-2} $year^{-1}$

Figure 3c. Trophic interaction in Site C (Hurandayan Bay, Guijalo, Caramoan Peninsula) seagrass system model



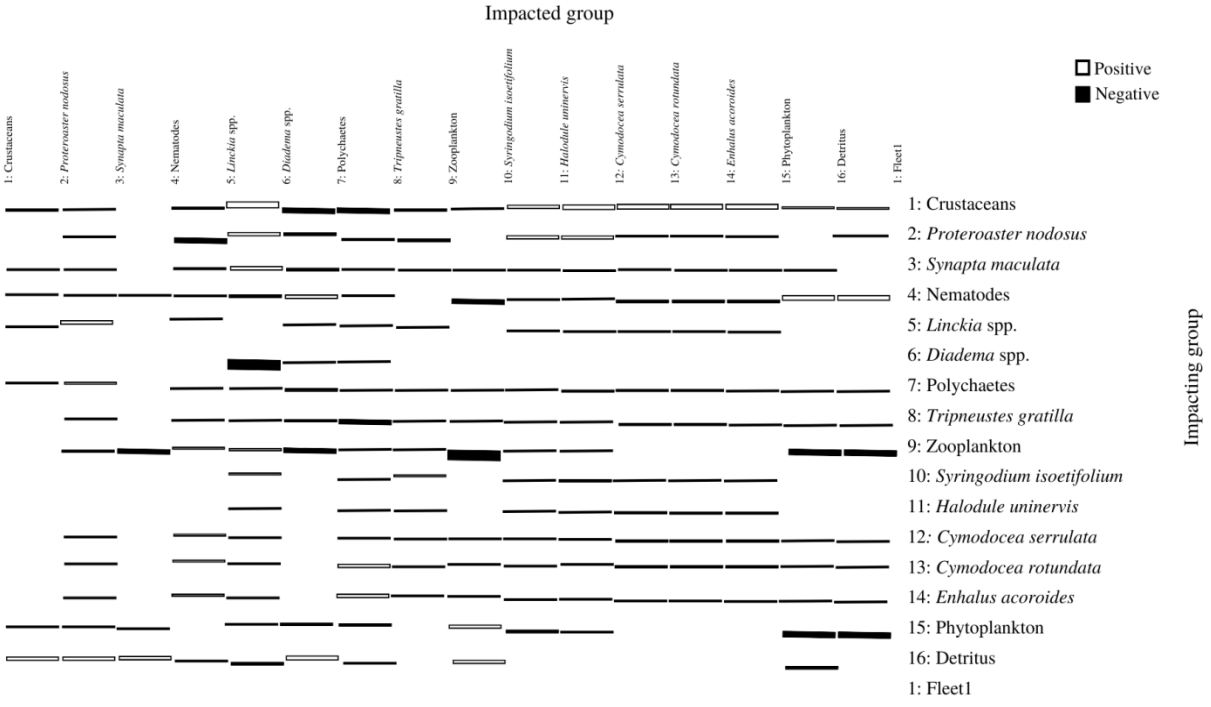
Black rectangles indicate positive impacts and white circles negative impacts.

Figure 4a. Combined direct and indirect trophic impacts of the functional groups in Site A (Lipata Bay, Lahuy Island, Caramoan Peninsula) seagrass system model



Black rectangles indicate positive impacts and white rectangles indicate negative impacts.

Figure 4b. Combined direct and indirect trophic impacts of the functional groups in Site B (Manlawi Bay, Lahuy Island, Caramoan Peninsula) seagrass system model



Black rectangles indicate positive impacts and white rectangles indicate negative impacts.

Figure 4c. Combined direct and indirect trophic impacts of the functional groups in Site C (Hurandayan Bay, Guijalo, Caramoan Peninsula) seagrass system model

3.2. Ecotrophic Efficiency (EE)

EE is the proportion of the production consumed by predators or exported to other ecosystems (Tables 1a, 1b, and 1c). All consumers have EE closer to 1, which shows the full utilization of the animals. However, the primary producers in the system, such as seagrasses and phytoplankton, including detritus, are underexploited.

For all three sites: (1) pristine, isolated, and sheltered seascape (Site A, Lipata Bay); (2) increased connectivity with mangroves (Site B); and (3) increased connectivity with corals (Site C), the seagrasses and phytoplankton with their EEs less than 0.08 indicate that a significant part of the production just accumulates to decreased consumption by the herbivores and grazers. Thus, supply exceeds demand. The excess production simply goes to detritus.

3.3. Trophic Flows

A single flow diagram that depicts all flows and biomasses can be generated from the mass balance ecosystem models constructed using EwE [12]. The flow diagram for the seagrass meadows is given in Figures 3a, 3b, and 3c. It can be inferred from the trophic flow diagrams that both the grazing and detrital pathways are essential in seagrass meadows based on the flows from the phytoplankton and detritus.

The primary sources for flow to detritus are phytoplankton and seagrasses. Moreover, the large trophic values (3. 92 in Site A, Lipata Bay; 2.76 in Site B, Malawi Bay, and, 3.0 in Site C, Hurandayan Bay) indicate an advantage based on Odum [23] that there is enough food energy when the food chain is short.

3.4. Mixed Trophic Impact (MTI)

MTI is useful in analyzing the trophic impact on the functional groups' biomass when the biomass of other groups changed dramatically and medium or long-term changes in biomass [23]. The results of the MTI for the seagrass meadows included in this study are shown in Figures 4a, 4b, and 4c.

MTI analyses of the three sites: (1) pristine, isolated, and sheltered seascape (Site A, Lipata Bay); (2) increased connectivity with mangroves (Site B); and (3) increased connectivity with corals (Site C) showed that phytoplankton and detritus have a positive impact on most other groups. However, the greatest impact was observed on direct predators. For example, phytoplankton significantly positive impact on zooplankton. Detritus had a positive impact on *S. maculata*, *Diadema*, and polychaetes, but it has no impact on many seagrass beds [24]. Furthermore, the known seagrass grazer, *Tripneustes gratilla* has a significant negative impact on the seagrasses.

3.5. Ecosystem Status, Scale, Maturity and Stability

The seagrass systems' network statistics are shown in Table 3 to assess an ecosystem's status and an ecosystem's status, scale, maturity, and stability.

The total system throughput is up to 13,859.68 t km^{-2} $year^{-1}$ (Site A), 17,078.09 t km^{-2} $year^{-1}$ (Site B) and 17,018.76 t km^{-2} $year^{-1}$ (Site C), where internal consumption accounts for 4.68% (Site A), 17.46% (Site B), and 17.68% (Site C) of the total flows, respiration for 2.22% (Site A), 7.92% (Site B) and 8.06% (Site C), and detritus for 47% (Site A), 39.90% (Site B), and 38.89% (Site C).

The ratio between total primary production and total system respiration (TPP/TR) is 22.29 (Site A), 5.38 (Site B), and 5.39 (Site C) in the models suggesting that all the seagrass systems are still immature. TPP/TR as an index of ecosystem maturity of an ecosystem declines to 1.0 as an ecosystem develops toward a "mature" stage or when under perturbation and increases to more than 1.0 when the ecosystem is in the early developmental stage.

The Connectance Index (CI) and the System Omnivory Index (SOI) are expressions of how complex the inner linkages are within the ecosystem. It is also an indication of the stage of maturity of an ecosystem. The CI in the models has a value of 0.210 (Site A), 0.333 (Site B), and 0.228 (Site C), indicating that among the three seagrass systems, the one which is nearer the mangroves is more mature than the other two systems. However, the models present a value of 0.211 (Site A), 0.036 (Site B), and 0.161 (Site C) for the SOI, indicating the least complexity of inner linkage in Site B than with Site A and C.

In terms of Overhead (O) which is an index of ecosystem stability and an expression of the potential of a system to increase its Ascendancy (A) when faced with sudden perturbations. Among the seagrass meadows in Caramoan Peninsula, Site B, which is near the mangrove ecosystem, and Site C, which is nearest to the coral reefs, have almost the same Overhead (27,254 Ø, flowbits for Site B and 27,973 Ø, flowbits for Site C), which indicates that these seagrass systems are vulnerable and slow to recover from disturbances.

Table 3. Summary statistics and network flow indices of the seagrass system models of Caramoan Peninsula, Philippines

Parameter	Sites		
	A. Lipata Bay	B. Malawi Bay	C. Hurandayan
Ecosystem theory indices			
Sum of all consumption (t km^{-2} $year^{-1}$)	649.28	2981.25	3009.123
Sum of all exports (t km^{-2} $year^{-1}$)	6386.87	5929.02	6019.934
Sum of all respiratory flows (t km^{-2} $year^{-1}$)	308.16	1353.42	1371.334
Sum of all flows into detritus (t km^{-2} $year^{-1}$)	6515.37	6814.40	6618.366
Total system throughput (TST, t km^{-2} $year^{-1}$)	13859.6	17078.09	17018.760
Sum of all production (t km^{-2} $year^{-1}$)	7079.708	8314.86	8421.922
Calculated total net primary production (t km^{-2} $year^{-1}$)	6868.44	7283.28	7385.958
Total primary production/total respiration (TPP/TR)	22.29	5.38	5.386
Net system production (PP-TR, (t km^{-2} $year^{-1}$)	6560.28	5929.86	6014.624
Total primary production/total biomass (PP/B, $year^{-1}$)	19.77	18.08	17.703
Total biomass/total system throughput (B-TST, $year^{-1}$)	0.025	0.024	0.025
Total biomass (excluding detritus) (t km^{-2})	347.50	402.79	417.212
Connectance Index (CI)	0.210	0.333	0.228
System Omnivory Index (SOI)	0.211	0.036	0.161
Ecopath Pedigree index	0.000	0.000	0.000
Information indices			
Ascendancy (A, flowbits) [%]	15060	18457	8001
Overhead (Ø, flowbits) [%]	13719	27254	27973
Capacity (C, flowbits) [%]	28779	45711	35975
Information (I)	1.087	1.081	0.674
A/C	0.523	0.404	0.222

3.6. Predicted Potential Future Changes of Seagrass Meadows

Ecosim modeling is anchored on the concept that changes in biomass of functional groups in the food web models could be predicted to respond to a scenario wherein exploitation mortality is distributed according to production and trophic levels. In this study, the scenario of exploitation mortality was simulated, following the approach done by Niera et al. [25] by distributing exploitation mortality according to production and trophic levels.

Human activities such as deforestation that led to increased nutrient loading and sedimentation may eventually lead to increased epiphyte growth in seagrass blades is a major problem in the Philippines. This scenario may lead to a bottom-up control system or resource-driven ecosystem wherein there are more ongoing interactions at the base or lower trophic level. In other seagrass meadows, the top-down control system or predator-driven ecosystem is more evident. This happens when there is overstocking of some economically important species, like sea urchins, that feed on seagrasses that result in the drastic demise of seagrasses which in turn has a negative impact on other animals that depend on the seagrasses as shelter or nursery ground. But the combination of bottom-up and top-down control seagrass systems is the typical scenario. These were the scenarios simulated in the Ecosim modeling.

The projected changes in the seagrass system model groups' biomass under simulated proportionally distributed exploitation along with trophic levels for the three sites, Site A (Lipata Bay), Site B (Manlawi Bay), and Site C (Hurandayan Bay), Lahuy Is., Caramoan Peninsula) are shown in Figures 5-7.

Seagrasses will have significant changes in their biomass for the next 15 years in all three sites. In Site A, a significant decline in biomass is expected for the benthic invertebrates (*Synapta maculata*, *Linckia* spp., *Tripneustes gratilla*) and a significant increase in biomass for the top consumer, *Proteroaster nodosus*. Although a minor decrease in biomass among consumers is expected in Site B, generally, no significant changes in biomass in

either the producers or consumers are expected for the next 15 years. In Site C, only the *S. maculata* and *Linckia* spp. are expected to significantly decline in biomass while the biomass of crustaceans will increase significantly. The increase in the biomass of top consumers is expected since their predators were not observed to be present and included in the models.

4. Discussion

Based on the maximum TL in the system, *Protoreoaster nodosus* (Echinodermata; Asteroidea) and crustaceans constitute the top predators in the three seagrass meadows. *P. nodosus* generally feed on meiobenthos and microbial/microalgal films on sediment and seagrasses and gastropods, sponges, soft corals, and other small invertebrates [26].

Overall, the seagrass systems have a low mean trophic level indicating short food chain and lack of top predators in the system. This finding of the study differs from the assumption of the early "productivity hypothesis" of Elton [27] that long food chains are evident in more productive ecosystems. In the case of seagrasses, as shown in this study, high biodiversity does not necessarily equate to a stable or highly productive ecosystem. The short food chain in the seagrass meadows revealed in the study indicates that the meadows could be considered to have a relatively small ecosystem size and community organization, following the argument of Vander Zanden et al. [28] and Post et al. [29] and. Food webs with longer food-chain lengths might be more vulnerable to shortening due to perturbations [30], hence we can assume the seagrass meadows focused on the study are not susceptible to perturbations. The findings confirm that the availability of energy or resource at the base of the food web and trophic efficiency in the seagrass meadows significantly influence the complexity of the food web and length of the food chain as suggested by Kaunzinger and Morin [31] and Post [32].

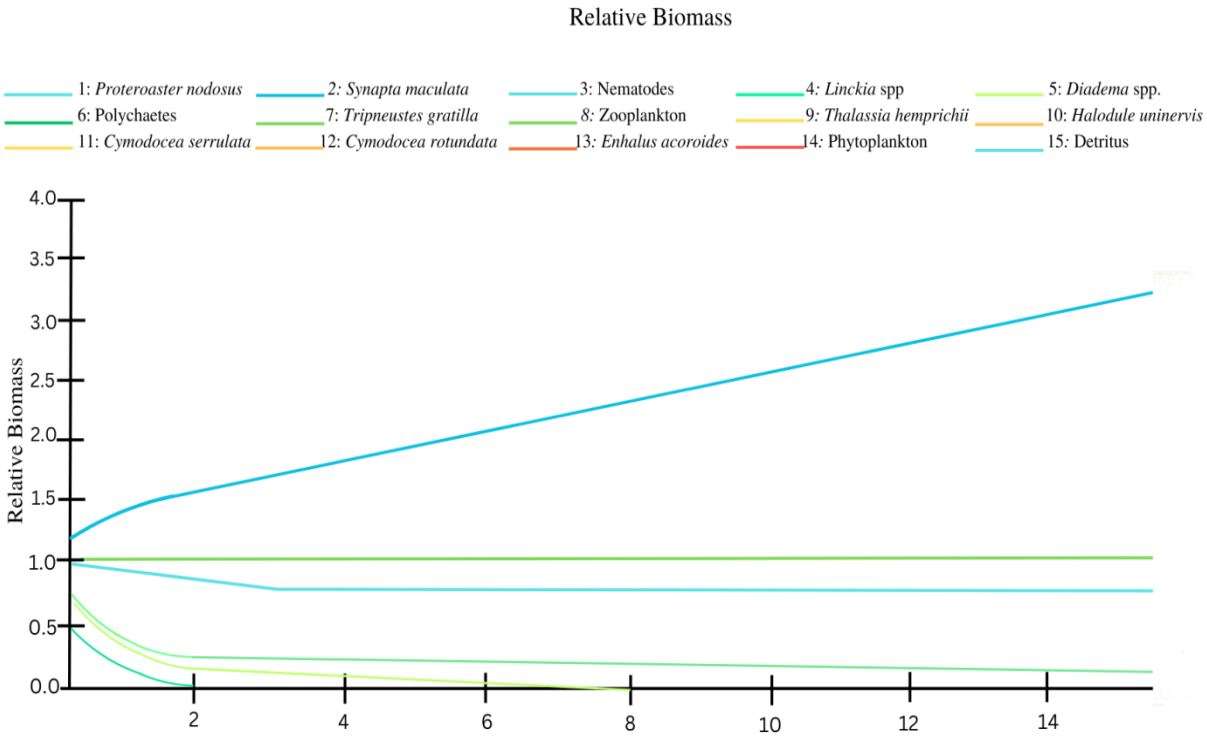


Figure 5. Projected changes in Site A (Lipata Bay, Lahuy Is., Caramoan Peninsula) seagrass system model groups' biomass under simulated proportionally distributed exploitation along trophic levels

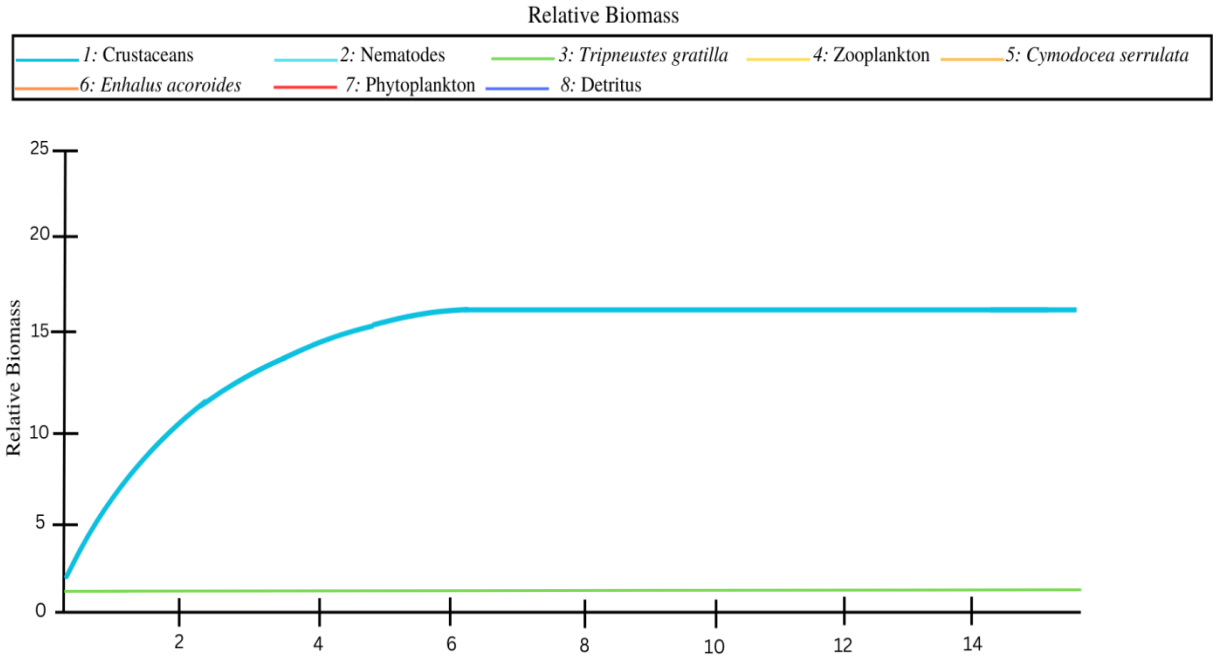


Figure 6. Projected changes in Site B (Manlawi Bay, Lahuy Is., Caramoan Peninsula) seagrass system model groups' biomass under simulated proportionally distributed exploitation along with trophic levels

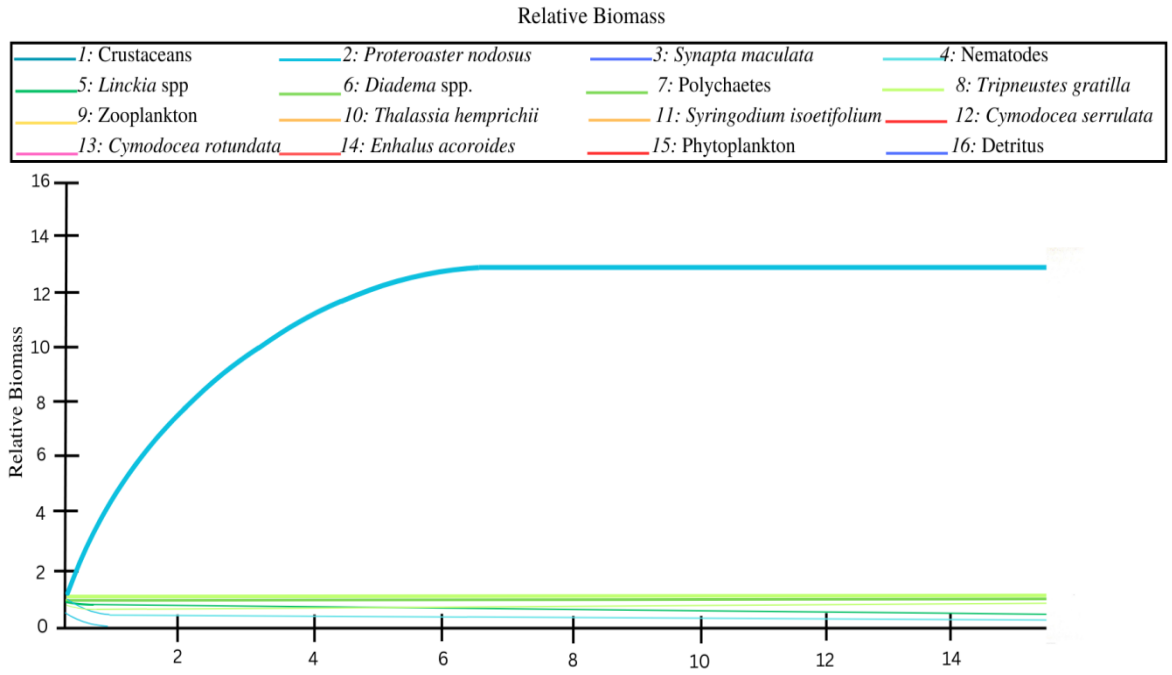


Figure 7. Projected changes in Site C (Hurandayan Bay, Guijalo, Caramoan Peninsula) seagrass system model groups' biomass under simulated proportionally distributed exploitation along with trophic levels

The Ecosim modeling showed that the primary producers typically have relatively higher EE values than top predators. However, this study shows that for the seagrass systems in Caramoan Peninsula, the EE values are high for most of the consumers, suggesting that these groups have a crucial role in the food web and may be challenged by high predation risk. The findings corroborate the results of previous studies [21] that trophic cascades could occur due to the increase in the biomass or density of primary producers because of diminished consumer density due to predation. Moreover, it can be inferred that in the seagrass meadows, the consumption of prey is not involved in the top interaction.

The absence of top predators that are the source of predation risk to the consumers (i.e., prey) lowers the chances of alteration in the predator-prey interaction that could occur in the seagrass meadows. In addition, this predation risk relates strongly to the findings that the seagrass meadows have a short food chain because predation risk can affect the size of food webs by restricting the flow of energy [35] or result in low productivity [36] or indirect effects of the size of these ecosystems [29].

The relatively low EE values for the detritus group indicate that the consumption is exceeded by biomass accumulation. The lower EE values for seagrasses suggest that there are few grazers in the ecosystems. Low EE value for the other invertebrate benthic groups in the three meadows indicates the groups were not fully consumed. Thus, the three seagrass systems have ecological efficiency, indicating a significant amount of energy available for transfer in the food chain. This result confirms the abundance of detrital pools in seagrass meadows as shed biomass, and sea bottom accumulation [37]. Moreover, the biomass accumulation in seagrass meadows shown in this study supports Zieger and Benner [38] and Peduzzi and Herndl [39] that the decomposition of necromass and living tissues, resulting in the detritus abundance in many coastal ecosystems.

The seagrass meadow near the mangroves has lower seagrass species richness but has higher biomass compared with the meadow near the coral reefs and the meadow located in a pristine, isolated, and sheltered seascape. This is consistent with Poovachiranon and Chansang [40] that seagrass ecosystems that are near mangroves ten have higher percentage cover and biomass, as observed for seagrass species associated with mangrove ecosystems off Thailand coast in Andaman Sea.

EE is the proportion of the production consumed by predators or exported to other ecosystems. All consumers have EE closer to 1, which shows the full utilization of the animals. However, the primary producers in the system, such as seagrasses and phytoplankton, including detritus, are underexploited. For all three sites, the EEs of seagrasses and phytoplankton indicate that a significant part of the production just accumulates to decreased consumption by the herbivores and grazers. Thus, supply exceeds demand, that is, the excess seagrass production simply goes to detritus. These findings are congruent with the observations of Mengistou [41] and Clores and Cuesta [8], who documented that herbivore grazers leave significant excess during the consumption of their prey. Furthermore, this finding implies that the production of seagrass is high, but a large amount of this production becomes part of unconsumed detritus. This could be the reason for the high total system throughput (TST) and detrital pathways in the seagrass bed models. It further indicates that the seagrass meadows still have available trophic space to accommodate more consumers. Lastly, in this scenario, it is anticipated that the energy in these meadows arises from detritus than primary production [42].

The single flow diagram that depicts all flows and biomasses generated from the mass balance ecosystem models also illustrates the grazing and detrital pathways based on the flows from the phytoplankton and detritus. Also, phytoplankton and seagrasses are primary sources of flow to detritus. The large trophic values indicate an advantage based on Odum [23] that there is enough food energy when the food chain is short.

The results of MTI analysis were consistent with the observations of Clores and Cuesta [8], showing that phytoplankton and detritus have a positive impact on most other groups. Phytoplankton significantly positively impact zooplankton illustrating that the greatest impact was observed on direct predators. Detritus had a positive impact on *S. maculata*, *Diadema*, and polychaetes, while the known seagrass grazer, *Tripneustes gratilla* has a significant negative impact on the seagrasses. Valentine and Heck [43] explained that most grazers in seagrass meadows feed preferentially on epiphytic algae, hence grazing is crucial in the maintenance of seagrasses over their epiphytes and the health of seagrass ecosystems. This result further implies that the presence of invertebrate grazers means a strong top-down influence on the seagrass system. Grazers contribute therefore to the major fraction of total secondary production in seagrass meadows, and their production predicts in turn the production of higher trophic levels.

In terms of the status, scale, maturity, and stability of the seagrass systems, the Connectance Index (CI) and the System Omnivory Index (SOI) indicate the stage of maturity of an ecosystem. The meadow located near the mangroves is more mature but with the least inner linkage than the other two systems. Based on Overhead (O) and Ascendancy (A) indices, the seagrass meadow near the mangrove and coral reefs appears to be vulnerable and slow to recover from disturbances compared with the pristine and isolated meadow. These results corroborate the findings that the total system throughput is highest in the seagrass meadow located closer to the mangroves and lowest in the pristine and isolated seagrass meadow. It similarly affirms the observation that the ratio between total primary production and total system respiration

suggests that all the seagrass systems are still immature. Clores and Cuesta [8] made the same conclusion about the other seagrass meadows in Caramoan Peninsula.

The Ecosim modeling shows that in a pristine and isolated seagrass meadow, a significant decline in biomass is expected for the benthic invertebrates (*Synapta maculata*, *Linckia* spp., *Tripneustes gratilla*) and a significant increase in biomass for the top consumer, Proteroaster nodosus. In a seagrass meadow near mangroves, a minor decrease in biomass among consumers is expected for the next 15 years. In a seagrass meadow near coral reefs, only the *S. maculata* and *Linckia* spp. are expected to significantly decline in biomass while the biomass of crustaceans will increase significantly. The increase in the biomass of top consumers is expected since their predators were not observed to be present and included in the models. These results support Pauly et al. [44] that the change in the species means trophic level (i.e., the diet composition of a species or a change in population structure combined with different ontogenic TLs), and/or a change in the relative abundance of each species.

In this study, the hypothesized bottom-up system, also considered resource-driven (habitat availability or resources being food) emphasizes the lower trophic levels and the significant factors that drive interactions at the base of the food web. An example would be the changes in the seagrass meadows due to nutrient loading from land run-off causing increased epiphyte growth on seagrass blades. The abundance of epiphytes (algae) may sooner or later increase the population of herbivores or mesograzers that eventually led to an increase also in their predators. On the other hand, the hypothesized top-down controlled system, also considered a predator-driven system, focuses on how top consumers (e.g., invertebrates) in the seagrass systems affect lower trophic levels, particularly the seagrasses. For example, if the sea urchin population increase due to overstocking, more sea urchins graze on seagrasses resulting in a decrease in seagrass cover, which may eventually affect other grazers or other invertebrates that use seagrass as nursery ground or habitat refuge. Lastly, to address the issue that the distinction between bottom-up and top-down control mechanisms constitutes a false dichotomy in the ecological sciences [23], a mixed flow control system simulation (Scenario 3) was done. It is assumed that in mixed flow control systems, bottom-up and top-down forces act simultaneously, that is the producers and consumers are resource-limited.

Considering the findings, the three seagrasses must be given appropriate management based on the findings (e.g., trophic structure and flows, ecotrophic efficiency, MTI, and network flow indices). The pristine and isolated seagrass meadows should be given more protection since they have no significant connectivity with other ecosystems (e.g., coral reefs and mangroves) that could have contributed to their stability and resilience. Seagrass meadows near mangrove forests require peculiar management that should maximize their potential as a refuge for crustaceans and other economically important invertebrates. Seagrass meadows located closer to the coral reefs, which have relatively similar indices to the meadow near mangroves, will also require conservation measures to ensure that this seagrass system becomes less susceptible to stress-induced changes and recovery from unexpected perturbations.

Indeed, the Philippines' coastlines face the negative impact of industrial development, high nutrient loading, and increased sedimentation. While the awareness of the importance of protecting, monitoring, managing, and restoring is increasing, realistic estimates and measurements of seagrass meadow parameters such as maintenance, loss, and expansion rates remain difficult. The present study provides important information, estimates, and projections needed for the poorly understood direct and indirect impacts on seagrass meadows, their species distribution, abundance, and connectivity with other ecosystems such as coral reefs and mangroves. Nonetheless, the interplay of other factors, e.g., biophysical processes, interactions, and the complexity of seagrass beds shall remain impediments to accurate prediction of the fate of seagrasses [45].

Verifying the predictions made in this study may be done by prolonged monitoring of the seagrass systems and conducting in situ experiments that shall demonstrate and very the projections of modelling and simulations.

5. Conclusions

The steady-state trophic (Ecopath) models of the seagrass ecosystems which were developed helped characterize the impact of biomass changes in each component of the seagrass systems in three seagrass meadows of Caramoan Peninsula: (1) pristine, isolated, and sheltered seascape; (2) increased connectivity with mangroves; and (3) increased connectivity with corals. The food web models were useful in predicting the impacts of biomass alterations in the three varied scenarios.

The constructed models were robust enough to predict the knock-on effects (i.e., alterations in the biomass under simulated proportionally distributed exploitation along with trophic levels) of higher and ecologically valuable trophic levels on the producer compartments. The MTI analysis of the model also identified the cumulative effects of consumer compartments on the producer compartment (i.e., seagrass) and vice versa.

Finally, information about the stability and resilience of the seagrass systems was derived from the network flow indices as the biomass functions. The hypothesis is that the three different scenario simulations resulted in varied biomasses and trophic interactions that revealed insights into possible management options of the seagrass systems.

Given the results (e.g., trophic structure and flows,

ecotrophic efficiency, MTI, network flow indices, and Ecosim dynamic models), the three seagrasses must be given attention so that these are conserved and protected. Although all are immature systems, Site A (Lipata Bay) should be given more management due to its vulnerability that cannot be afforded by the presence or connectivity of other ecosystems (e.g., coral reefs and mangroves). The seagrass meadow nearest to the mangrove forest (Site B, Manlawi Bay) needs more unique management to maximize its potential as a refuge for crustaceans and other economically important invertebrates. The seagrass meadow closest to the coral reefs (Site C) can also be considered conservation sentinels since it is less susceptible to stress-induced changes and recover from unexpected perturbations than the other seagrass meadows.

All the seagrass meadows can be recommended for mitigation efforts including the creation of buffer zones in the meadows so that the distance between the seagrass, mangroves, and coral reefs as sensitive habitats are maintained and lessened impact. There is a need to further examine the models and simulations through calibration and validation through actual field experiments to rehabilitate denuded habitats, if any, can be. Monitoring studies of the status, stability, and maturity of the seagrass meadows is also recommended, along with community education about the role of seagrasses in a healthy coastal environment.

Acknowledgment

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